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Influencing Factors of Seed Long-distance Dispersal on a Fragmented Forest Landscape on Changbai Mountains, China

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Abstract: Seed long-distance dispersal (LDD) events are typically rare, but are important in the population processes that determine large-scale forest changes and the persistence of species in fragmented landscapes. However, previous studies focused on species dispersed via animal-mediated LDD, and ignored those dispersed by wind. The aim of this study was to assess the effects of canopy openness, edge, seed source, and patch tree density on the LDD of seeds by wind in forest. We collected birch seeds, a typical wind-dispersed species, throughout a larch plantation. We then assessed the relationship between birch LDD and each factor that may influence LDD of seeds by wind including distance to edge, canopy openness size, distance to mature forest, and the tree density of the larch plantation. We used univariate linear regression analysis to assess the influence of those factors on birch LDD, and partial correlations to calculate the contribution of each factor to LDD. The results showed that both canopy openness and edge had significant influences on birch LDD. Specifically, a negative relationship was observed between distance to edge and birch LDD, whereas there was a positive correlation between canopy openness size and LDD. In contrast, the distance to the mature forest was not correlated with birch LDD. Our results suggest that patch tree density could potently affect the probability of LDD by wind vectors, which provides novel and revealing insights regarding the effect of fragmentation on wind dynamics. The data also provide compelling evidence for the previously undocumented effect of habitat fragmentation on wind-dispersed organisms. As such, these observations will facilitate reasonable conservation planning, which requires a detailed understanding of the mechanisms by which patch properties hamper the delivery of seeds of wind-dispersed plants to fragmented areas.

Keywords: seed long-distance dispersal (LDD); forest fragmentation; patch property; wind dispersal; Changbai Mountains

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1 Introduction

Seed dispersal play a central role in the life history stage of a plant, which can affect the rate of species recruitment, species range expansion, and the overall spatio-temporal patterns of forest regeneration (Jordano and Herrera, 1995; Schupp and Fuentes, 1995; Wang and Smith, 2002; Thomson *et al*., 2011; Yu *et al*., 2013). Compared with seed long distance dispersal (LDD), much attention has been focused on the effects of short distance dispersal on forest dynamics. Plants through LDD sample more potential regeneration sites and minimize negative interactions with their siblings and mother (Soons and Ozinga, 2005). The frequency of LDD events are typically low, but are central to several population processes (Levin *et al*., 2003; Nathan *et al*., 2003), particularly large-scale processes such as population spread, the flow of individuals among populations, the colonization of unoccupied habitats, and community assembly (Nathan *et al*., 2003; Givnish and Renner,

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2004; Nathan, 2006).

As such, seed LDD, rather than local dispersal, determines changes in the large-scale forest, species distribution following climate change, and the persistence of species in fragmented landscapes (Levin *et al.*, 2003). In fragmented landscapes, LDD has a major influence on both plant species persistence (Farwig *et al.*, 2006; Herrera and Garcia, 2010; Sansevero *et al.*, 2011) and vegetation recovery when disturbance is reduced (Howe and Miriti, 2004). As a result, fragmented patch properties are receiving increased attention as a way to enhance both the LDD of individuals, and species persistence (Heller and Zavaleta, 2009; Krosby *et al.*, 2010). In addition, an increasing number of studies have assessed how the landscape fragment affects animal movement. Previous studies about tree seed dispersal tended to ignore species whose seeds are dispersed by wind, which was often assumed to not limit by dispersal.

Although short distance dispersal events can be empirically quantified, LDD events (the unusually long movements accomplished by only a small fraction of individuals in a population) are difficult to detect empirically. Gaining a mechanistic understanding of how habitat fragmentation affects seed dispersal by wind has been proven challenge. As a result, seed LDD events are typically predicted using mechanistic models. However, these predictions are rarely empirically tested, particularly for tree seeds that are dispersed by wind (Bullock and Nathan, 2008). Sufficient empirical data are necessary for model parameterization and calibration, and are also helpful for the further study of LDD.

In fragmented landscapes, a number of factors might influence the LDD of seeds by wind, such as the seed source, the canopy openness size of sample site, the distance to edge of fragmented patch, and patch properties. For seed sources, seed fall is highly concentrated around the seed source, with a rapid, often exponential, decline with increasing distance from the source (Harper, 1977; McClanahan and Wolfe, 1987; Portnoy and Willson, 1993; Willson, 1993). An increasing distance from the seed source reduced the frequency of seed LDD in most systems (Kirika *et al.*, 2008; Cordeiro *et al.*, 2009; Lehouck *et al.*, 2009). When canopy openness size is considered, large canopy openness might increase wind speed that may enhance seed dispersal distance and expand seed dispersal area (Damschen *et al.*, 2014). For distance to the edge, the probability of seed to go through might be limited from the edge to the centre of the patch, which might affect the LDD of tree seeds by the wind. The matrix type is often different at the edge, which might also affect wind speed, and subsequently affect the frequency of seed LDD. Fragmented patch characteristics such as tree density might influence the flow of matter in inter-fragmented patches. This might alter the wind speed which potentially influenced seed dispersal distance. However, few seed dispersal studies have directly considered the matrix as a conduit for seed movement (McConkey *et al.*, 2012). As such, it is important to clarify how different factors affect the LDD of tree seeds by wind to better understand the distribution mechanism of these species.

The Changbai Mountains form a typical cool temperate mixed forest ecosystem in the northern parts of the temperate zone. In this region, previous forest management was focused on timber harvest. The harvested species mostly were broadleaf species, which caused the abundance of rare broadleaf species to decrease sharply. Wind is a common dispersal mechanism used by most broadleaf species in this area. After trees were harvested for timber, the harvested areas were re-planted with larch, which made the landscape increasingly fragmented. If LDD can maintain species persistence in a fragmented landscape, then the factors in the fragmented areas that affect the frequency of wind-stimulated LDD of seeds in a larch plantation should be studied further. Such studies would also be useful to better understand the mechanism of the LDD of seeds by wind in other ecosystems.

Birch is a common broadleaf species that played a role in early succession of natural forest ecosystem on the Changbai Mountains. It has small-sized and low weight seeds that are mainly dispersed by wind. Understanding which factors affect birch seed LDD will shed light on the seed LDD of other wind-dispersed broadleaf tree species after landscape fragmentation. The development of reasonable conservation planning requires an understanding of the mechanisms by which different properties hamper the delivery of the seeds of such plants to fragmented areas.

The aim of this study is to assess the influence of canopy openness, edge, seed source, and planted tree density on the LDD of seeds by wind. We focused specifically on canopy openness size, the distance from the seed trap to the edge of fragmented patch, the tree density of the fragmented patch, and the distance to mature forest, which are all thought to be more important factors for seed LDD (Hewitt and Kellman, 2002). We assessed the correlation between the number of birch seeds that arrived at each seed trap and each of these factors. We had three major hypotheses. 1) Canopy openness size has a positive effect on the number of birch seeds that disperse. Therefore, a large gap facilitates seed arrival compared with a smaller one. 2) Sites close to the edge of fragmented patch can receive more seeds. 3) Sites far from the mature forest receive less seeds. To test these hypotheses we addressed the following questions. 1) How do each of these factors influence birch seed LDD? 2) Which factor is the most important for enhancing birch seed LDD? 3) Does the tree density of the fragmented patch affect birch seed LDD? In this study, we only focused on partial factors which potentially influenced LDD of seeds by wind. Other factors such as patch area and shape were not analyzed in our research.

2 Materials and Methods

2.1 Study area

The study area (42°20′–42°40′N, 127°29′–128°02′E) was located on the northwestern slope of the Changbai Mountains, northeastern China. The composition of the Changbai Mountains vegetation is more complex and the biodiversity is higher than other areas in the temperate zone. The forests in this region are comprised of Korean pine and broadleaf mixed forests, which are dominated by mixtures of Korean pine, Amur Linden (*Tilia amurensis*), Manchur Ash (*Fraxinus mandshurica*), and Mongol Oak (*Quercus mongolica*). Timber harvesting was the main activity in this forest system. As the demand for timber increased during the 1970s and 1980s, forests were harvested mainly by clear-cutting (Dai *et al*., 2009). After timber harvesting, most of the harvested areas were re-planted with larch (You *et al*., 2013). Fifteen years after re-planted, the larch plantations have implemented partial cutting, and thereafter left natural growing. Self-thinning and different growing rates of individuals occurred in these kind of stands. These factors caused different canopy openness size.

The sample sites were located in the Lushui River Forestry Bureau, which covers an area ~1.21 × 10^5 km^2 and ranges in elevation from 600–900 m (Fig. 1). The climate of the area is characterized by long, cold, windy winters and short, moist summers. The mean annual temperature is 2.8℃ and the annual precipitation is ~670 mm. Approximately 80% of total annual precipitation occurs between June and September.

2.2 Data and Processing

This work was performed based on the Forestry Standards ′Observation Methodology for Long-term Forest Ecosystem Research′ of the People′s Republic of China. This standard was processed by Chinese Forest Ecosystem Research Network (CFERN) and formed for managing data of long-term forest ecosystem research. We selected two monoculture larch plantation stands with different tree densities and the stand age was more than 30 years as sample sites. Surrounding of the plantations was composed by broadleaf mature forest. The shape of the plantation stands was polygon and the area of the plantations were 18 ha and 11 ha, respectively. We then established 53 seed traps at study area (Fig. 1). Detailed information regarding setting the seed trap is described below.

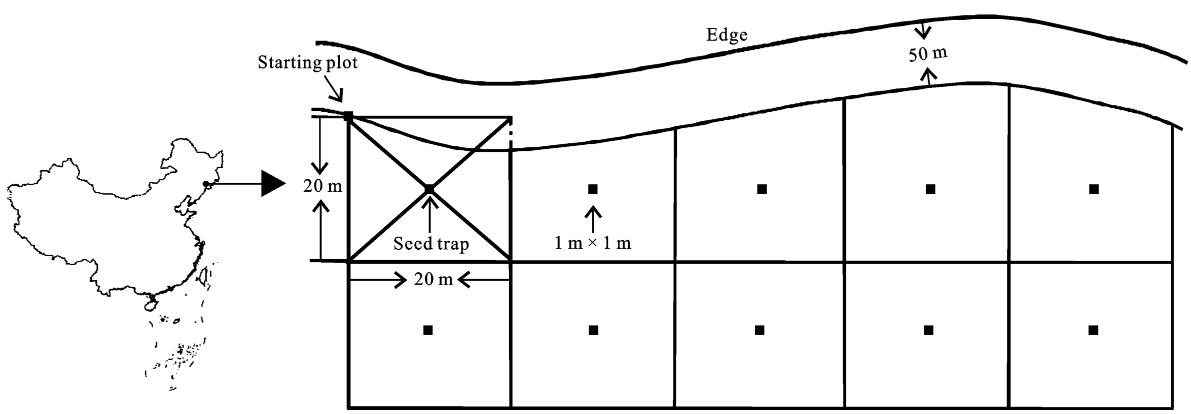

Fig. 1 Location of sample sites in Lushui River Forestry Bureau in northeast China, and illustration of seed trap setting

2.2.1 Seed traps

The seed traps were set as shown in Fig. 1. A point located 50 m from the edge of larch plantation surrounding by natural and mature broadleaf mixed forest was selected as the starting point to ensure that the collected birch seeds had arrived via LDD. We then extended the first line into the plantation vertical to the edge, and a node was set every 20 m along the edge to inner of plantation. We then set several lines at each node perpendicular to the first sample line. Several lines were also set parallel to the first sample line and the interval distance was set as 20 m. This formed a series 20 m × 20 m quadrats in the larch plantation, and a series of irregular polygon at the edge of the plantation. These irregular polygon and the 20 m × 20 m rectangular quadrats were treated equally in the investigation and analysis. Seed trap was arranged at the midpoint of each irregular polygon and rectangular quadrat. Each seed trap used in the present study was a 1 m × 1 m square made of fine, flexible 1-mm-thick mesh placed 1-m above ground, and was supported by four PVC tubes. Seeds were collected twice a month from May to December, and once a month from January to April, starting in May 2012 and ending in March 2013.

2.2.2 Canopy openness size

A digital hemispherical photography (DHP) method was used to estimate size of the openness of the forest canopy above each seed trap. The DHP system was based on a Canon 60D Digital SLR camera and a Sigma 8-mm F3.5 EX DG Fisheye lens. The DHP image could provide a 360° horizontal field of view, and a nearly 180° vertical field of view. The Can-Eye software (Version 6.0) manual was used to calibrate the DHP system and derive the parameters for establishing the project functions (Weiss, 2002). A first-order applicable project function, with a root-mean-square error < 0.5 pixel, was obtained. The Can-Eye software can derive canopy structure characteristics from true colour DHP images acquired from factors such as the leaf area index, and cover the fraction of canopy (fCOVER). It was designed to process several images at once with optimal performance (Blennow, 1995). In the current study, we collected nine upward DHP images from each sample site and performed image processing following the user manual instructions provided with Can-Eye software. Most images were acquired in cloudy weather to avoid underestimating the fCOVER caused by overexposure of the DHP images. The coefficient of the circle of interest was set as 30° to ensure that the area covered by the DHP images could match the spatial scale of the sampling site. Ultimately, the ratio of sky coverage for each sampling site was used as a surrogate of the canopy openness size.

2.2.3 Distance to edge

The geographical coordinates of each seed trap were recorded using a Global Positioning System (GPS). The coordinate data were then imported into the Geographic Information System (GIS) database of the study area. The distance of each seed trap to their nearest edge of plantation stand was calculated in the GIS. The distance data were used as distance to edge.

2.2.4 Distance to surrounding mature forest

GIS was also used to calculate the distance from each seed trap to the centre of the mature forest stand surrounding the larch plantation. We defined this distance as the distance of seed trap from seed source. This method can not quantify the accurate distance from seed trap to the mature tree. However, it may explain the influence of distance to mature forest on seed dispersal frequency.

2.3 Data analysis

Univariate linear regression analysis was used to quantify the marginal influences of canopy openness size, distance to edge, and distance to the mature forest on LDD of birch seed. To understand the relative contribution of edge, canopy openness size, and tree density of the larch plantation on birch seed LDD, partial correlations based on type III sums of squares were used to partition the variance in seed LDD among the unique contributions of edge, canopy openness, tree density of the larch plantation, and their overlap. Type III sums of squares derived from univariate analysis were used to quantify the relative importance of edge, canopy openness, tree density, and their interaction with birch LDD. Higher type III sums of square values indicated stronger contributions to seed LDD. Four regression models included different influencing factors were constructed. One of those regression models considered the tree density of the larch plantation as random factors. The Akaike Information Criterion (AIC) of each model was then compared to evaluate whether the tree density of the larch plantation influenced birch seed LDD.

3 Results and Analyses

3.1 Influence of each factor on seed LDD

Results revealed that both canopy openness size and distance to the edge had significant relationships with birch seed LDD. There was a negative relationship between distance to edge and birch seed number which represented frequency of birch seed LDD (Fig. 2). A seed trap far away from the edge was often accompanied by a low seed arrival rate. In contrast, there was a positive relationship between canopy openness size and birch seed number (Fig. 3), suggesting that a large canopy openness size increased the seed arrival rate. However, the distance to the mature tree stand was not correlated with birch seed LDD. The correlation of canopy openness size and distance to edge with seed number varied between the two sample sites. The distance to the edge had more effect on seed LDD in the high-density sample site compared with the low-density sample (Fig. 2). Similarly, the effect of canopy openness size on seed

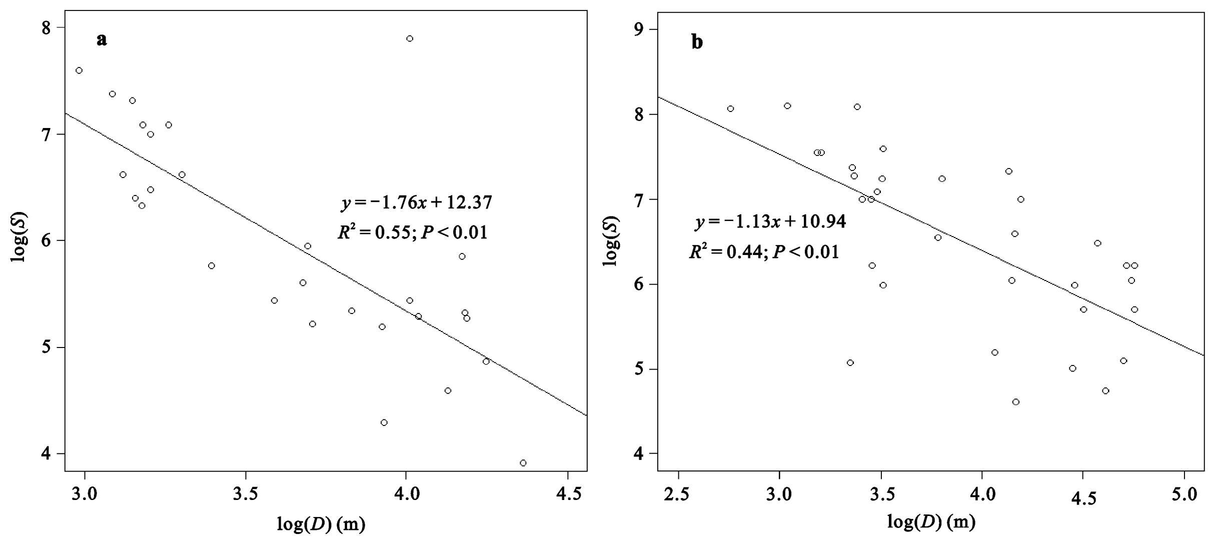

Fig. 2 Scatterplots showing relationship between distance to edge of larch plantation and long-distance dispersed seeds. This relationship was analyzed at high tree density (a) and low-density (b) sample sites. Each point represents the value for an individual site. The relationships between variables are showed well liner correlation. The solid lines show the fitted linear trend lines. *D*: distance to edge; *S*: seed number

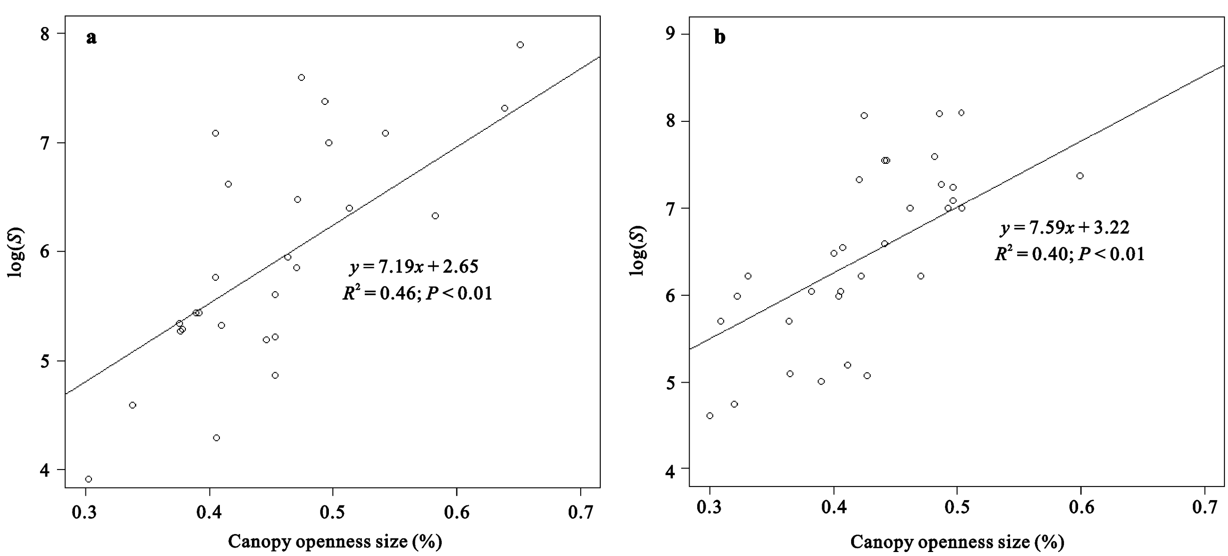

Fig. 3 Scatterplots showing relationship between canopy openness size and long-distance dispersed seeds. This relationship was analyzed at high tree density (a) and low-density sample sites (b). Each point represents the value for a site. The relationships between variables are showed well liner correlation. The solid lines show the fitted linear trend lines. *S*: seed number

LDD was greater in the high-density sample than at the low-density site (Fig. 3). Compared with distance to edge, the variation in canopy openness size was small between sample sites. The distance to the mature tree stand had no effect on seed number at either the low or high intensity sample sites (Fig. 4).

3.2 Influence of each factor and their overlap on seed LDD

Proportions of actual type III values were used to compare the relative importance of distance to edge, canopy openness size, and density of plantation on birch seed LDD. Result showed that distance to edge had the strongest effect on seed LDD. Variance partitioning analysis revealed that distance to edge, canopy openness size, and their interaction together explained 65.7% of the seed number, with distance to edge alone accounting for 33.6% of the variance (Fig. 5). Canopy openness size alone explained 13.2% of the seed number variance, whereas larch density at the sample site explained only 8.6% of the variance. Seed LDD was mainly affected by the distance of the seed trap to the edge, followed by canopy openness size. Larch density at the sample site also had influence on seed LDD. The interaction effects of canopy openness size and distance to edge were more important than other interaction effects to seed LDD, which explained 18.9% of the seed number variance. Although larch density at the sample site alone was not very important for seed LDD, its interaction with other factors had more effect on birch LDD, and explained 25.5% of the variance.

3.3 Influence of tree density on seed LDD

Whether tree density at the fragmented patch affected LDD was examined by adding tree density as a stochastic term to a regression model, followed by a mixed general linear model to calculate the AIC. Low AIC value means the regression model has high degree of fitting. The AIC of different regression models revealed that adding tree density of the two sample sites as random factor to the linear regression model could obviously decrease the AIC (Table 1). After adding tree density to the model, the AIC decreased by ~16. Therefore, the tree density may influence the seed arrival rate.

Table 1 Regression models used to evaluate whether adding tree density as a stochastic term has influences on LDD through their Akaike Information Criterion (AIC) values

Regression model	AIC
$y=ax_1$	157.8
$y=ax_2$	158.2
$y=ax_1+ax_2$	147.4
$y=ax_1+ax_2+\varepsilon$	131.2

Notes: y: seed number; x_1: gap size; x_2: distance to edge; ε: tree density

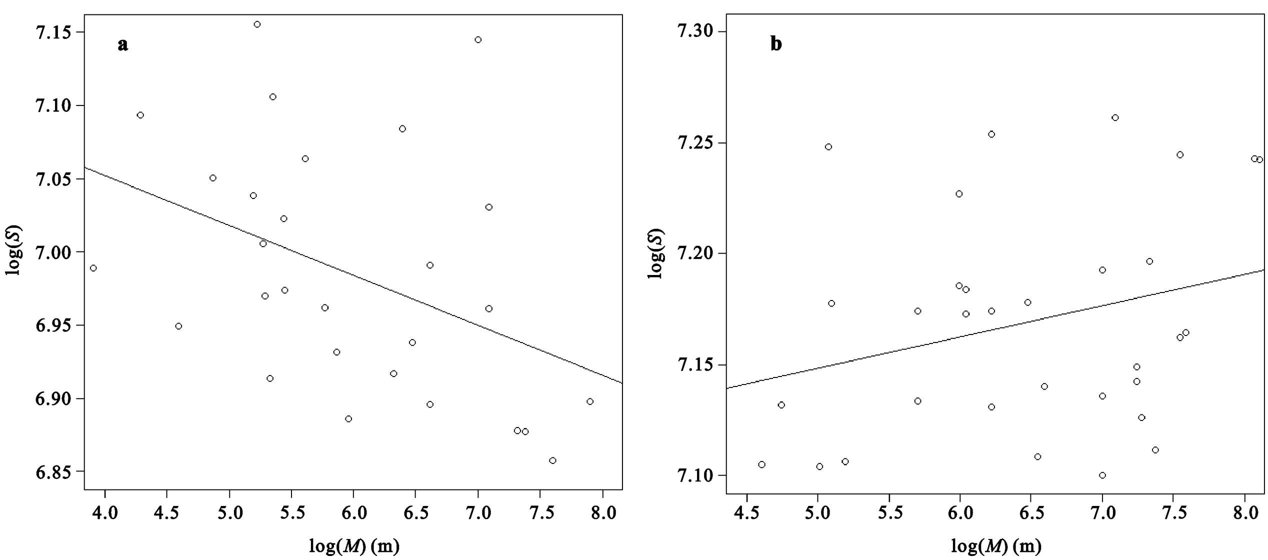

Fig. 4 Scatterplots showing relationship between distance to mature tree stand and long-distance dispersed seeds. This relationship was analyzed at high tree density (a) and low-density (b) sample sites. Each point represents the value for an individual site. The solid lines show the fitted linear trend lines. *M*: distance to mature tree stand; *S*: seed number

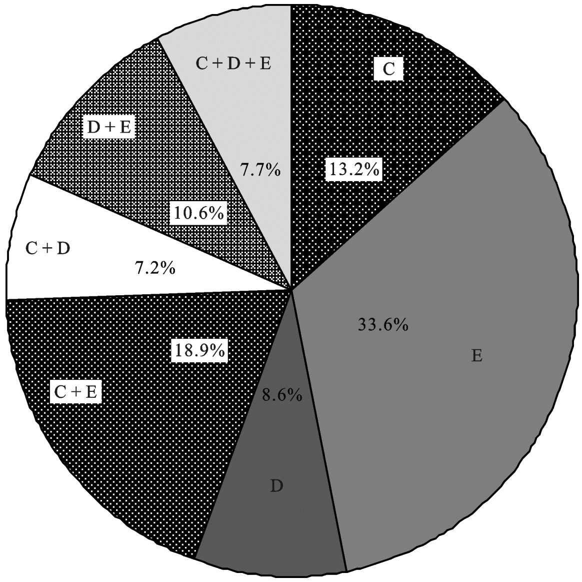

Fig. 5 Relative contributions of distance to edge (E), canopy openness size (C), tree density at sample site (D), and their overlap on long-distance dispersed seeds as measured by type III sums of squares

4 Discussion

Seed density declines monotonically with distance from the seed source (Muller-Landau *et al*., 2008). Previous studies assessing dispersal curves indicated that, beyond a certain distance, seed density did not change significantly with distance from the seed source (Nathan and Muller-Landau, 2000). The LDD determines the regional survival and establishment of species after disturbance (Malanson and Armstrong, 1996; Valverde and Silvertown, 1997; Hanski, 1998; 1999). More importantly, it also largely determines the rate of population spread (Kot *et al*., 1996; Clark, 1998; Levin *et al*., 2003; Soons and Ozinga, 2005; Pergl *et al*., 2011). Habitat fragmentation limits the short seed dispersal across the landscape. However, based on a dispersal curve reported previously, habitat fragmentation had little effect on LDD (Herrera and Garcia, 2010).

Wind is a frequent means of movement for many organisms, including plant seeds, pollen, spores, insects, and pathogens (Howe and Smallwood, 1982; Foissner, 2006; Friedman and Barrett, 2009). The changes in habitat structure (e.g., edge creation) that accompany habitat fragmentation might strongly influence the flow of air, particularly the amount of vertical uplifting, which is a critical factor known to drive the LDD of seeds by wind (Nathan *et al*., 2002; Tackenberg, 2003; Bohrer *et al*., 2008). However, fragmentation properties are almost exclusively considered a conservation strategy for animals or animal dispersed organisms, and not for the great diversity of species that are passively transported by the wind. The results of the current study showed that fragmentation properties had significant effects on wind seed dispersal. Canopy openness size was positive correlated with seed LDD, so that a large void space could enhance the number of seeds that arrived seed trap. This might be because an open canopy accelerates wind speed relative to the closed one, increasing the probability of LDD of seeds by wind.

Habitat openings have three distinct effects on wind dynamics, redirecting, bellowing, and ejection hotspots, which might also alter wind speed (Damschen *et al*., 2014). Distance to edge also affected the probability of seed LDD in the fragmented landscape. The strongest enhancement of wind speed occurs at the edge of fragmented patches because the wind in these areas experiences less drag relative to that in the surrounding forest matrix due to the lack of tree-canopy obstacles (Nathan and Katul, 2005). As such, the plots in the current study near the edge of the fragmented patches could receive more birch seeds than those in the centre of patches. Other fragmentation properties such as the tree density in each patch could potently affect the probability of LDD of seeds by wind. Tree density changed the wind characteristics via the altered matrix flow rate inside the patch. Previous data suggested that this effect is strongest close to the ground, affects the wind direction in the patches close to the matrix, and is weaker above the canopy (Damschen *et al*., 2014). A previous study demonstrated that the distance to the mature tree stand is one of the most important factors that influence seed dispersal (Hewitt and Kellman, 2002). However, the results of this study showed that the distance to the mature tree had no effect on wind seed LDD, which might be because the amount of birch seeds is large, the number of seeds arrived seed trap may not limit by hundred meters distance from mature tree. The other reason might be the number of seeds dispersed was constant beyond a certain distance from the parents.

Unlike animal-dispersed species, whose richness is affected by corridors, patch shape and matrix density are more important for species that dispersed by wind (Damschen *et al*., 2008). The current study revealed that canopy openness size, distance to edge, and the tree density of the patch influenced the richness of the species seed LDD by wind. Importantly, wind-driven dispersal is rarely considered during reserve design and planning. However, our results suggest that patch shape which has great influences on distance from seed trap to patch edge and matrix density strongly affect the movement of wind-dispersed seeds. The data from this study could also be used to elucidate wind dynamics and dispersal in other ecosystems, including forested patches in an open matrix, and for other wind-dispersed organisms.

Several limitations should be pointed out when interpreting and extrapolating the results of this study. First, we only collected birch seeds over a 2-year period. Interannual variation of seed production might alter the effect of fragmentation properties on birch LDD. We assumed that the interannual variability of seed production might not change the relationship between fragmentation properties and LDD. As such, the results of this study must be extrapolated with caution. Second, the only fragmentation properties assessed were canopy openness size, tree density, and distance to the edge and mature trees. We did not analyze other properties such as variations in topography, which might also affect birch seed LDD via altered wind speed. Finally, our seed trap was set in a larch plantation. As such, we did not address whether variations in forest type affected wind seed LDD.

We demonstrated that habitat fragmentation alters wind dynamics in multiple ways that can be predicted using models and can be used to determine the LDD of seeds, as well as predict the apparent consequences for the plant community. These findings provide novel insights regarding the influence of fragmentation on wind dynamics, compelling evidence for a previously unreported effect of habitat fragmentation on wind-dispersed organisms, and novel evidence for how the landscape structure might mediate patterns of species richness by altering dispersal.

5 Conclusions

From the results we know fragmentation properties could potently affect the probability of seed LDD by wind, which provides novel and reveals insights regarding the effect of fragmentation on wind dynamics. We found that distance to edge and canopy openness size had more influences on the probability of seed LDD by wind in which distance to edge was the most important factor. Different with normal assumption that seed LDD was correlated with distance to mature tree stand, there was no significant correlation of probability of seed LDD by wind with distance to mature tree stand which because the specific property of birch seeds. Birch seeds was small with low weight, and the amount was large. We also found tree density has influences on seed LDD by wind. However, in this paper we did not quantify this influence. Our results could provide compelling evidence for the previously undocumented effect of habitat fragmentation on wind-dispersed organisms. These observations will facilitate reasonable conservation planning, which requires a detailed understanding of the mechanisms by which fragmentation properties hamper the delivery of seeds of wind-dispersed plants to fragmented areas.

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